

Action-matching biases in monkeys (*Sapajus spp.*) in a stimulus-response compatibility task:
Evaluating experience-dependent malleability

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Abstract

Stimulus-response compatibility effects occur when observing certain stimuli facilitate the performance of a related response and interfere with performing an incompatible or different response. Using stimulus-response action pairings, this phenomenon has been used to study imitation effects in humans, and here we use a similar procedure to examine imitative biases in non-human primates. Eight capuchin monkeys (*Sapajus spp.*) were trained to perform hand and mouth actions in a stimulus-response compatibility task. Monkeys rewarded for performing a compatible action (i.e., using their hand or mouth to perform an action after observing an experimenter use the same effector) performed significantly better than those rewarded for incompatible actions (i.e., performing an action after observing an experimenter use the other effector), suggesting an initial bias for imitative action over an incompatible S-R pairing. After a predetermined number of trials, reward contingencies were reversed; i.e., monkeys initially rewarded for compatible responses were now rewarded for incompatible responses, and vice versa. In this second training stage no difference in performance was identified between monkeys rewarded for compatible or incompatible actions, suggesting any imitative biases were now absent. In a second experiment, two monkeys learned both compatible and incompatible reward contingencies in a series of learning reversals. Overall, no difference in performance ability could be attributed to the type of rule (compatible/incompatible) being rewarded. Together, these results suggest that monkeys exhibit a weak bias towards action copying, which (in line with findings from humans) can largely be eliminated through counter-imitative experience.

Keywords: stimulus-response compatibility, imitation, social learning, capuchin monkeys.

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To imitate, an animal may recreate, through action, the perceived visual qualities of the act they see performed by another. However, the visual information obtained from perceiving another animal's actions often does not correspond to the sensory experience of observing one's own performance of the same action; indeed, sometimes an action is entirely opaque to the actor (e.g., when performing a facial expression). The cognitive challenge in overcoming this so-called correspondence problem (Nehaniv & Dautenhahn, 2002) might explain why researchers examining action imitation (more specifically defined as converting "visual information into matching motor acts", Custance, Whiten, & Fredman, 1999, p. 14), in nonhuman primates, have concluded that there is a qualitative difference in comparison with human abilities (Call & Tomasello, 1995; Frigaszy, Deputte, Cooper, Colbert-White, & Hémery, 2011; Subiaul, 2016; Tennie, Call, & Tomasello, 2012; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Indeed, the question of imitative ability in animals dates to early work in the comparative tradition (Thorndike, 1911), and has continued in more recent times (Caldwell & Whiten, 2002), however, even those who claim nonhuman apes might possess some capacity to imitate are more cautious when describing the abilities of monkeys (Whiten & van de Waal, in press).

Over the last decades, researchers of social learning have documented many failed attempts to observe action imitation in monkeys (e.g., Frigaszy et al., 2011; for reviews see Frigaszy & Visalberghi, 2004; Visalberghi & Frigaszy, 2001), yet studies using simple, extractive foraging tasks have provided some evidence that monkeys will match the body part used by a conspecific to open containers. Voelkl and Huber (2000) found that common marmosets (*Callithrix jacchus*) were more likely to open a box with their hand after observing

a conspecific use the same body-part, when compared to individuals who had seen the container opened by mouth. Furthermore, a detailed frame-by-frame analysis of the video footage of these actions found that specific action characteristics measured when the monkeys opened the box with their mouth (e.g., head inclination) were significantly more alike when one monkey had watched another perform the action (in comparison to monkeys who had not observed a conspecific; Voelkl & Huber, 2007). Using a similar methodology with a larger sample of vervet monkeys (*Chlorocebus aethiops*), van de Waal and Whiten (2012) provided further evidence of body-part matching. Subjects were more likely to use their hand after observing a conspecific use that same action when opening a food-baited canister. These studies of bodily imitation in a few species of monkeys provide the extent of positive findings on motor imitation in adult monkeys, although evidence of a distinctive form of imitative behavior, which may be unrelated to the current question of imitation in adult monkeys, has also been reported in neonates (e.g., Ferrari et al., 2006).

Developmental approaches to imitation suggest certain types of experience are crucial for imitative ability to develop. For example, the associative sequence learning approach and ideomotor approach posit that imitative ability is formed through compatible sensorimotor experience; i.e., the contingent experience of performing and observing the same action (Heyes, 2010; Heyes & Ray, 2000; Prinz, 1997, 2005). This sensorimotor experience could occur when an infant observes their own actions or by being imitated by caregivers (Del Giudice, Manera, & Keysers, 2009). Support for experiential accounts of imitation has been provided through the use of stimulus-response compatibility (SRC) procedures that incorporate stimulus-response action pairs. With human adults, an action SRC task requires participants to perform two different actions (e.g., hand opening/closing) while simultaneously presented with a task irrelevant image that displays either a compatible action (i.e., the action they must perform) or an incompatible action (i.e., the different action). Reaction times (RTs) are

consistently quicker when the image presented corresponds with the action to be performed, while images of incompatible actions invoke slower responses, a phenomenon described as automatic imitation (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000). This action-specific SRC effect is similar to those found in traditional SRC procedures, where stimuli-response pairs share other overlapping characteristics (e.g., spatial location, Simon & Rudell, 1967; or semantic content, e.g., Stroop, 1935; for a review see Kornblum, Hasbroucq, & Osman, 1990), and has been proposed as a method of studying imitation, mimicry, and mirror neurons in humans (Heyes, 2011).

If some forms of imitation are modulated by sensorimotor experience, it follows that these imitation effects are malleable and should be influenced by sensorimotor training; indeed, incompatible training sessions, where participants were required to open their hand after seeing a hand close and vice versa, delivered 24 hours before an action SRC task has been found to significantly reduce compatibility effects in adult humans (Heyes et al., 2005). Catmur et al. (2008) used a similar method to examine activity in brain regions associated with mirror neuron activity, and after incompatible training (performing hand actions when presented with an image of a foot and vice versa), brain areas previously related with hand actions were active when viewing images of a foot, possibly suggesting that the neural substrates thought to facilitate imitative behavior (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al., 1999), are sensitive to experience. This evidence suggests that existing cognitive relationships between sensory-motor representations, whether innate or learned, are plastic, and can adapt to varied inputs. While a nativist and empiricist approaches to imitation are not necessarily mutually exclusive, a proper understanding of the impact of experience on imitation in

nonhuman primates is currently lacking, which presents a stark contrast with the efforts devoted to investigating pre-existing abilities.

With human participants, SRC effects identified using action S-R pairings are examined using reaction time measurements. They occur when participants (required to perform specific responses), are unintentionally and automatically influenced by action stimuli in accordance with the compatibility state of the S-R pairing (Brass et al., 2000; Catmur & Heyes, 2011; Stürmer et al., 2000). Compatible S-R pairings therefore typically facilitate performance (fast RTs), whereas incompatible pairings tend to produce interference (slower RTs).

Studies that have examined this SRC effect in nonhuman animals follow a different approach (Mui, Haselgrove, Pearce, & Heyes, 2008; Range, Huber, & Heyes, 2011). Instead of examining RT response, subjects are trained to respond with two different actions discriminatively to two action stimuli, and associations between stimuli and responses are learned by trial and error. Learning success is then compared between compatible (i.e., rewarded for performing the action they see) and incompatible S-R pairings (i.e., rewarded for performing a different action to the one they see), and if compatible pairings are learned more quickly than incompatible pairings, it is inferred that the perceptual qualities of the action stimulus aids in the performance of that same action over a different action, indicative of some imitative ability or bias. Given the training procedure, it is less clear that the compatibility effects can be said to be “automatic” and so the term automatic imitation may be less suited to these findings (although to date, the comparative literature has been described using this same terminology; i.e., Mui et al., 2008; Range et al., 2011).

Using this comparative methodology, budgerigars (*Melopsittacus undulates*) rewarded for imitating a conspecific perform a foot versus a beak action have been found to learn the associative rule more quickly than subjects rewarded for performing an opposite action (Mui

et al., 2008). Similarly, domestic dogs (*Canis lupus familiaris*) rewarded for opening a door with the same body part as their owner (hand/paw or mouth), learned this rule faster than those rewarded for using the opposite body part (Range et al., 2011). Furthermore, in the study of imitative biases in dogs, it was found that once the animals were reinforced for incompatible rules, their subsequent performance on compatible actions was poorer when compared to dogs that had not experienced incompatible training. The authors concluded that this suggests that previous incompatible experience carried over into the subsequent condition where only imitation was rewarded, which is consistent with experiential accounts of imitative ability. The use of these learning procedures provides a method of assessing whether S-R associations relevant to bodily imitation are facilitated by compatibility effects, thus providing a means by which underlying biases can potentially be revealed.

Here, our aims are two-fold. Firstly, using an SRC paradigm, we will examine if capuchin monkeys find compatible S-R actions pairings (i.e., when hand actions are rewarded following presentation of a hand-action stimulus, and mouth actions are rewarded following presentation of a mouth-action stimulus) easier to learn in comparison to incompatible pairings (i.e., when hand actions are rewarded following presentation of a mouth-action stimulus and vice versa). Capuchin monkeys are New World primates that interest researchers of social learning because of their high brain to body-mass ratio (see Frigaszy, Visalberghi, & Fedigan, 2004), socially tolerant nature (Fragaszy, Feuerstein, & Mitra, 1997), tool use capacities (Visalberghi, 1993), and evidence of socially learned traditions in wild populations (Perry, 2011). Capuchins have been studied extensively to examine their social learning abilities (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Fragaszy et al., 2011; Visalberghi & Addessi, 2001) yet no clear evidence of action imitation has been identified in this species (e.g., Fragaszy et al., 2011). However, though previous studies suggest capuchin monkeys learn primarily from non-imitative forms of social learning (Craist, Hardy, &

Fragaszy, 2010; Fragaszy et al., 2011; Galloway, Addessi, Fragaszy, & Visalberghi, 2005) the methodology employed here will permit investigation of more subtle imitative biases. Secondly, if imitative biases are present in capuchins we hope to examine whether this bias is resistant to counter-imitative training.

In a first experiment we address both of these aims. Capuchin monkeys were rewarded for performing actions with their hand and mouth discriminatively upon observing an experimenter perform hand and mouth actions. Half of the monkeys were reinforced for performing the same action they observed the experimenter perform (i.e., performing hand actions to hand stimuli; mouth actions to mouth stimuli), and the other monkeys were rewarded for performing the alternative action. We predicted that if capuchin monkeys enter into this procedure with some bias to imitate specific motor actions they would perform better when rewarded for the compatible rule. Following this first set of training, the reinforcement of S-R contingencies was reversed; i.e., monkeys that were initially rewarded for compatible responses were rewarded for performing incompatible responses, and vice versa. If capuchin monkeys possess a strong disposition to imitate (whether learned or innate), it might be expected that during this reversal-learning stage those learners switching from an incompatible rule to a compatible rule should perform better than individuals that experience the alternate reversal.

Experiment 1: Two-action stimulus response compatibility task

Methods

Subjects and research site

Eight capuchin monkeys (*Sapajus spp.*) were tested in experiment one (six males; mean age at the beginning of the study was 3.9 years, SD = 2.0; range = 1.4 - 7.5). All monkeys were

housed in one of two mixed-species groups with squirrel monkeys (*Saimiri sciureus*) at the Living Links to Human Evolution Research Centre at Edinburgh Zoo, Scotland. The monkeys were never food- or water-deprived, and all rewards offered during research sessions were supplementary to their diet. Before this experiment took place these capuchins had been studied on a range of cognitive tasks (e.g., Morton, Lee, & Buchanan-Smith, 2013), however, no previous study had examined action imitation. Ethical approval was granted by the University of Stirling Psychology Ethics Committee, and all research took place between February 2011 and June 2012.

Materials

Eight research cubicles arranged in a connected 2X4 matrix act as a corridor between the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm X 52.1 cm X 51.4 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their groupmates for research purposes. The cubicle window (i.e., the Perspex screen orientated toward the experimenter) included a small opening in its center, allowing juice to be delivered to the capuchins through a mouthpiece connected to a rubber-tube and syringe. On the bottom left side of the cubicle window was a hole (3.5cm diameter) through which food rewards were offered. To shape two disparate actions a modified table tennis paddle was used (see Electronic Supplementary Material, ESM, Video 1.). Alternate sides were colored black and white to facilitate color discrimination training. A second target was used during the stimulus response compatibility (SRC) trials that differed in shape and color (see ESM Video 2). Sessions were recorded on a Sony Mini DV Digital Video Camera.

Shaping behaviors

For monkeys to take part in SRC trials, two actions employing disparate body parts were trained: touching the cubicle window with a) their hand and b) their mouth. These specific

actions were used as they were considered similar to those used in previous comparative work (Mui et al., 2008; Range et al., 2011), but also trainable through reinforcement. These actions are not incompatible in the sense of their performance being mutually exclusive (e.g., opening versus closing a hand), but the use of disparate body parts is common practice when studying imitation in primates (e.g., Voelkl & Huber, 2000), as well as stimulus-response compatibility effects in humans and other animals (Catmur & Heyes, 2011; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Mui et al., 2008; Range et al., 2011). The training of both actions took place concurrently through positive reinforcement of successive approximations of each action.

To train each individual to touch the cubicle window with their mouth, diluted fruit juice (one part juice to two parts water) was delivered from a syringe to the mouthpiece on the inside of the cubicle. Capuchins learned to bring their mouths to the screen to receive the juice reward. Next, the experimenter presented the training target ~5cm in front of the window before the juice was delivered. Once capuchins learned to bring their mouths to the window before the juice was delivered, the juice reward was replaced with a food reward. In some instances the monkeys would use their hands to balance themselves against the Perspex screen when performing the mouth action, but this action was still interpreted as a mouth action as the goal was to place their mouth against the screen. To train a distinct hand action the training target was presented to the small hole where food rewards were offered. The target was removed once touched by the subject's hand and a food reward was offered. Gradually, the target was moved further from the hole, and the subject, unable to touch the target directly, was rewarded for touching the window with one or two hands. A monkey was never rewarded for a hand action if their mouth was also presented to the screen. At this point the learned association between stimulus and action was spatial in nature (the mouth action cued by the target presented near

the center of the window; the hand action cued by the target presented nearer the left of the window).

Color discrimination learning

Once actions had been shaped and were performed reliably to spatial cues the target was only presented in the center of the window and to be rewarded the capuchin was required to learn a color association rule (see ESM Video 1). The same target (see ESM Video 1) was used to cue both actions, but a different colored side was used in each case (i.e., for four monkeys the black side was always presented when training hand actions and the white side was always presented during the training of mouth actions; the opposite color/action pairing was reinforced for the other four monkeys). Only correct responses were rewarded, i.e., performing an action that corresponded to a specific color, and if an incorrect response was performed the experimenter turned his back on the monkey for approximately three seconds, a form of negative punishment, removing the opportunity to receive further rewards for a short time-period. Once an individual had performed over 85% correct responses on three consecutive research sessions (20 trials per session), the monkey began the SRC trials.

Stimulus Response Compatibility Trials (SRC)

Upon completion of the color discrimination trials, individuals were transferred into one of two groups: a compatible condition or incompatible condition. During these stimulus response compatibility trials, the color stimulus was switched for an action stimulus (i.e., instead of seeing a black target or a white target on a given trial, the monkey would see the experimenter touch a target with either his hand or his mouth). Based on performance in the initial color discrimination stage, groups were counterbalanced to include equal numbers of quick discrimination learners (mean number of research sessions before reaching criterion on

the color discrimination task was 45.75 for subjects in the compatible condition and 45 for subjects in the incompatible condition). On each research session we attempted to complete twenty SRC trials with each monkey, however, monkeys could end the research session by demonstrating cues to leave and so some sessions included fewer trials. During an SRC trial a second target (see ESM Video 2) was held in front of the experimenter with his left hand and touched with either a) his right hand or b) his mouth. The target was then moved to ~5cm in front of the window. The number of hand and mouth actions performed by the experimenter was kept equal throughout these sessions, i.e., 10 mouth and 10 hand actions, and the order of hand and mouth stimuli was pseudorandomized (the maximum number of repeats was one; e.g., the stimuli performed in half an SRC session might proceed as follows: Hand(H)-Mouth(M)-H-H-M-H-M-M-H-M). Individuals in the compatible condition were rewarded for performing actions using the same body part as the experimenter; i.e., if the experimenter touched the target with his hand, the monkey was rewarded for performing an action with their hand; and if the target was touched by the experimenter's mouth, the monkey was rewarded for using their mouth). Individuals in the incompatible condition were rewarded for using the opposite actions; if the experimenter touched the target with his hand, the monkey was rewarded for performing an action with their mouth, and vice versa.

If an action response was ambiguous (i.e., hand placed against the window on its own, and quickly replaced with a mouth response), the target was removed by the experimenter and the trial was repeated. A correct response was rewarded with a food item, and an incorrect response resulted in the experimenter turning his back on the monkey for approximately three seconds. Actions were judged to be correct/incorrect by the experimenter during the research session but all sessions were video recorded for subsequent reliability coding. A random sample of 550 action responses (6%) were extracted from video recordings and information

about the action performed by the experimenter (i.e., action stimulus presented) and trial outcome (i.e., whether monkey was rewarded) was removed. These actions were re-coded by the same experimenter that had conducted the experiment, and although this individual was not naïve of the hypotheses, the removal of contextual cues made it impossible to know whether an action performed by a monkey was in response to the same action or a different action. Agreement between the experimenter's decision within the research session and without contextual information was high ($Kappa = .97$; $p < .001$). Once a predetermined learning criterion was reached ($\geq 85\%$ correct responses in three consecutive 20 trial sessions) the reward contingency was to be reversed. However, only one monkey had reached this criterion before 900 trials, and due to time constraints, monkeys were switched to the opposite condition regardless of progress after 900 trials, and a further 500 trials were completed by each monkey. Two monkeys were tested on fewer trials in each condition to examine performance on both associate rules without the potential confounding effects of overtraining (320 trials in each condition). As monkeys were free to leave in the middle of sessions and the goal of each session was to test monkeys with 20 trials, monkeys completed on average 10.4 trials more than the established cut-off.

It is worth noting that throughout this action stimulus stage we continued to conduct some color discrimination trials to confirm that each subject could still perform both trained actions discriminately. For example, before performing any SRC trials during a given session, four color discrimination trials were completed (color discrimination trials were also performed after the 10th SRC trial and after the 20th trial). We continued to reward this already learned association to encourage participation and to assess an individual's ability to perform both hand and mouth actions discriminately.

Data Analysis

The monkeys' success on each trial was recorded as a binary response variable (either correct or incorrect). This binary variable was used as the outcome variable in a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to test specific hypotheses concerning imitative biases in the SRC paradigm. As each monkey received multiple trials in each condition, the monkey being tested was included as a random intercept in the GLMMs. Furthermore, session number (i.e., consecutive blocks of 20 trials) was included as a random slope in the models. To test hypotheses concerning the persistence of an imitative effect, a model was created with an interaction included for condition and order of learning. To describe the contribution of predictor variables to trial success, odds ratios were calculated by back-transforming the log odds ratios. All statistical tests were conducted with the R statistics program (R Core Team, 2014) in the Rstudio environment (RStudio Team, 2014). Models were developed using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015), and graphics were created using the ggplot2 package (Wickham, 2009). Monkeys completed up to 900 trials in the first block of learning, but only the first 500 trials for each monkey were examined (320 in the case of two monkeys), for two reasons. Firstly, one monkey's associative rule was switched after 500 trials, so a comparison between groups is balanced at this point (see ESM, Figures 1 and 2 for all performance data summarized for each monkey- areas highlighted in light grey were analyzed). Also, to examine any pre-existing bias in automatic imitative ability it is more appropriate to examine earlier performances.

Results

Overall, monkeys were biased towards mouth actions, performing this action in 54.54% of all analyzed trials. Every monkey developed an effector preference at some stage of the experiment; i.e., the same action was used consistently across a session. For example, when

looking at diversity of action performance, we find that across all monkeys and testing sessions, on average, 90.9% of responses within a 20-trial session consisted of one type of action (although this bias could alternate across sessions; e.g., a monkey that performs mainly hand actions in one session might change to mouth responses on the following session). As trial success in this context is unlikely to be related to a learned association between a specific stimulus and response, and as overall success above a 50% chance level requires a diversity of actions, effector was not examined as a predictor of success.

Descriptive data on overall performance for each monkey can be found in Table 1 (also see ESM, Figures 1 and 2 for all performance data plotted chronologically by session). A GLMM found a significant interaction between the rule being rewarded (compatible/incompatible) and the order in which the rule was learned (Wald test, β [condition x order] = 0.298, s.e. = 0.148, $z = 2.012$, $p = 0.044$; see Table 2 for full model; see Figure 1). In the first block of discrimination learning the chance of success was significantly lower when learning an incompatible rule (an estimated 22.81% lower odds of being correct, confidence intervals, 95% CIs: 1.33% - 39.62%; Wald test, β [incompatible] = -0.259, s.e. = 0.125, $z = -2.067$, $p = .039$; see Figure 1 when order = first), but in the second block of learning (i.e., after associative rules were switched), the type of associative rule being rewarded did not influence chance of success (Wald test, β [incompatible] = 0.039, s.e. = 0.076, $z = 0.512$, $p = .608$, see Figure 1 when order = second; estimated 3.99% greater odds of success on an incompatible trial, CIs: -10.47% – 20.79%).

Discussion

When monkeys first learned an association between an action stimulus and an action response, individuals reinforced for a compatible rule performed significantly better than those who were reinforced for an incompatible rule. This finding is the first evidence of a

compatibility effect in an action SRC paradigm with nonhuman primates, contributing to existing comparative evidence in birds and dogs (Mui et al., 2008; Range et al., 2011), although it is important to highlight that this initial effect is weak (i.e., estimated CIs = 1.33% - 39.62%), and that only one monkey reached the predetermined learning criterion. The difficulty in learning a compatible action association is consistent with previous work with capuchins that has shown that while certain types of behavior matching is possible (e.g., action that requires the movement of objects), actions themselves are rarely copied (Fragaszy et al., 2011).

We found that the marginally superior performance of those rewarded for compatible responses in the first learning block did not persist once reward contingencies were reversed, which suggests that reinforcing certain stimulus-response associations (whether compatible or incompatible S-R associations) subsequently makes it equally difficult to learn the reversed associative rule. The comparable lack of success observed in both conditions in the second block of learning is consistent with predictions of an experience based account of imitation and similar effects observed in humans and other animals (Heyes et al., 2005; Range et al., 2011). However, as only one monkey learned an associative rule (i.e., reaching the predetermined criterion), and as we may have ended training in the second block before a compatibility effect was identifiable we conducted a second experiment to further examine the possibility of a predisposition for imitative ability. In this study we retested two monkeys from experiment one on a series of reversal learning sets to examine if a compatibility bias would be more evident in a repeated reversal design. Using the same SRC procedure used in experiment one, each monkey learned both compatible and incompatible action rules to a predetermined criterion. The small sample used in this second experiment may limit the scope of our conclusions, but if a bias to imitate is present in capuchin monkeys we may expect that following rule reversal, performance on the compatible associative rule would be overall better than on the

375 incompatible rule.

376 **Experiment 2: Repeated reversal learning of a stimulus-response association**

377 **Methods**

378 **Subjects**

379 This second experiment examined repeated reversal learning of compatible and
380 incompatible rules with two male monkeys from experiment one (Chico: 3.4 years and
381 Carlos: 6.2 years at the beginning of experiment 2). These monkeys were selected for this
382 experiment as they were the best learners in the initial learning blocks of their respective
383 conditions (see first block in Table 1). These research sessions took place between October
384 2012 and July 2013, ten months after Carlos' last session in experiment one, and four months
385 after Chico's last session.

386 **Procedure**

387 Both monkeys were tested in a similar fashion to experiment one. In the first block of
388 learning Chico was rewarded for performing incompatible responses and Carlos was rewarded
389 for performing compatible actions. Correct responses were rewarded with a food item and
390 incorrect responses resulted in a three second time-out where the experimenter would turn their
391 back to the monkey. One strategy employed by monkeys in experiment one in an effort to
392 maximize rewards was to perform one action repeatedly (see Results of experiment 1),
393 therefore receiving half of all rewards in each research session. To improve speed of learning
394 and to encourage switching between actions, correctional procedures were introduced. If
395 monkeys responded incorrectly on a trial the same trial was repeated until the monkey either
396 performed the correct response or an incorrect response was performed a certain number of
397 times. We expected that these training procedures would increase the likelihood that a rule will

be learned more quickly by forcing monkeys out of single-action biases. Furthermore, we kept these procedures consistent across conditions, so that they would not interfere in interpreting performance. Initially, a trial was repeated up to five times if an incorrect action was performed, however, five consecutive “time-outs” became an overly stringent punishment and subject participation dropped. To increase participation, incorrect responses were instead repeated 3 times (this change occurred after 264 trials for Chico, and after 78 trials for Carlos). These incidences were always scored as a single incorrect trial.

Learning criterion in this second experiment was altered as it was felt that the initial criterion was unnecessarily strict and may have interfered with the identification of learning in some cases. In the second experiment, to qualify as having learned an associative rule, monkeys had to progress through the following stages. First, a monkey had to provide 65% or more correct responses on a test session consisting of twenty trials. Once this criterion had been met, on subsequent testing sessions monkeys were only tested on ten trial sets. To demonstrate evidence of learning, monkeys had to perform 80% or more correct responses on two consecutive sessions of ten trials (taking place at different testing sessions; i.e., a minimum of an hour between testing). This two-tier criterion was employed as we wanted to offer monkeys sufficient experience of the reward contingencies in the earlier stages of learning. However, we noticed in experiment one that monkeys would sometimes lose interest with the procedure after performing a number of consecutive correct responses (possibly due to satiation). It was predicted that reducing session length to 10 trials during later stages of learning would improve motivation to attend to the procedure and would therefore provide a better measure of learning. Furthermore, this 80% criterion was still highly unlikely to be reached by chance (i.e., 16 correct responses in 20 trials is likely to occur by chance only 1.2% of the time), and so, while

we believe that reducing the criteria would not have made the rule easier to learn it may have made it easier to identify when a monkey had learned the rule.

Once this criterion was met, the associative rule being rewarded was reversed. Over the course of the experiment, Carlos reached the required criterion for the compatible rule three times and the incompatible rule twice, and Chico reached the criterion for both conditions twice. To retain comparable numbers of learning blocks for each monkey, Carlos' first four blocks of learning were analyzed. Throughout these SRC sessions we continued to begin each session with 4 color discrimination trials, to encourage participation and to ensure monkeys could perform both actions discriminately.

Data analyses

The first response to each trial was coded as a binary response variable (correct or incorrect) – correct responses to a repeated trial were not counted. Furthermore, as monkeys reached criterion at different stages for each block of learning we examined the initial performance over the first 60 trials of each learning block. This analysis criteria serves both the function of having a comparable number of trials to compare for both Carlos and Chico (i.e., 240 trials per monkey), and a comparable number of incompatible and compatible trials (i.e., 240 trials per condition). Using a generalized linear model (GLM) with a binomial distribution and logit link function, the effect of condition (compatible/incompatible) and individual subject were examined. This analysis would determine whether an associative rule is easier to switch to after having reached a predetermined number of correct responses on the other associative rule (see above). The interaction between associative rule being rewarded (compatible versus incompatible) and subject was examined to see if performance on conditions was independent of individual monkey.

Results

For descriptive data on the number of trials it took each monkey to reach the learning criteria on each learning block see Table 3. A GLM identified a significant interaction between condition and monkey (Wald test, β [monkey x condition] = 1.722, s.e. = 0.392, $z = 4.390$, $p < 0.001$; see Table 4 and Figure 2). There was no difference in performance between conditions for Chico (estimated 15.98% higher odds of success in the incompatible condition, CIs: -32.00% - 97.83%; Wald test, β [incompatible] = 0.148, s.e. = 0.273, $z = 0.544$, $p = 0.586$) and Carlos performed significantly worse on incompatible trials (odds of a correct response were 79.28% lower in the incompatible condition, CIs: 63.97% -88.08%; Wald test, β [incompatible] = -1.574, s.e. = 0.282, $z = -5.576$, $p < 0.001$).

Discussion

In this second experiment, further efforts to examine imitative biases in two capuchin monkeys showed no evidence that imitative rules are intrinsically easier than counter-imitative rules over a series of learning reversals sets. As a complement to experiment one we demonstrated that both compatible and incompatible action rules can be learned by two capuchin monkeys, but that overall it is not easier to learn one associative rule over the other. One monkey did perform better when compatible trials were rewarded when compared to incompatible trials, but without further study of a larger sample, we cannot conclusively state whether this finding is driven by an imitation bias, or a bias towards a first-learned association (although, the second monkey in experiment two showed no bias towards either rule).

General Discussion

In our first experiment, we report the first evidence from nonhuman primates of an imitative bias in an action stimulus response compatibility (SRC) task. In general, evidence of action imitation in monkeys is scarce, but this result complements evidence of bodily matching

reported in New World (Voelkl & Huber, 2000, 2007) and Old World monkeys (van de Waal & Whiten, 2012). It is worth highlighting that only one monkey reached the predetermined criterion in the initial learning block, and that in general, the difficulty that monkeys faced in transferring their previously learned color-action association skills to an action-action associative paradigm demonstrates that this imitative bias is not necessarily automatic in the sense of being reflexive and effortless. At least, the ability to match hand and mouth actions are not readily available to capuchin monkeys (also evidenced by previous research; e.g., Frigaszy et al., 2011). Indeed, it has been argued that the ability to imitate actions may not be present in any non-human primates (Tennie, Call, & Tomasello, 2009), at least in a manner that does not require considerable training or human enculturation (e.g., Custance, Whiten, & Bard, 1995). Instead, the effect identified here may be an implicit bias that this specific procedure could tap into, and may be related to some other, non-imitative, form of social influence, such as those identified in more naturalistic contexts in primates (e.g., mimicry, response facilitation; Mancini, Ferrari, & Palagi, 2013). Given the many reinforcement trials received across these studies, the difficulty the monkeys faced in reaching the learning criteria in either condition might be puzzling. It is unclear, however, whether this problem stems from an imitative deficiency, or rather a more general problem related to the saliency of action stimuli, or short-term memory capacities for action stimuli. A more general perspective on how imitative learning fits within other domains of social cognition is largely lacking and future work with SRC methods may help understand how imitation fits within this broader context.

We recognize that our protocol traded ecological validity for control over stimulus presentation and ease of interpreting action responses, and so future studies may identify stronger imitative effects in more naturalistic contexts (i.e., foraging contexts). Furthermore, the use of a human demonstrator may have influenced attentional or other factors, and although

human demonstrators have been used in studies of imitation (Custance et al., 1995; Frigaszy et al., 2011), mirror neurons (Gallese et al., 1996; Keysers et al., 2003), and imitation recognition (Paukner, Suomi, Visalberghi, & Ferrari, 2009), the greater control facilitated by the use of an SRC task may be improved with the use of a conspecific demonstrator. In spite of how these factors were likely to have contributed to the difficulty these monkeys faced when learning this task, we demonstrated that two monkeys were able to meet a strict learning criterion in experiment two. This provided confirmation that, given enough experience, capuchins can learn to distinguish between specific human actions and respond discriminatorily. Indeed, the initial compatibility bias suggests that even in an ecologically artificial set-up, capuchin monkeys must have, to some degree, been sensitive to the correspondence between observed actions and the performance of actions using the same body-part, at least initially.

The controlled nature of this method, that incorporated a prolonged testing phase taking place over a number months, allows a more nuanced exploration of action matching when compared with previous efforts with primates (e.g., Voelkl & Huber, 2000; van de Waal & Whiten, 2012) where action matching is assessed from behavior that immediately follows a single observation period (for good reason, as behavior at later stages is confounded by individual learning). We believe that future work incorporating elements of our method, with a wider range of actions and stimulus-response contingencies, could be useful in determining both the action matching abilities of primates and the role of experience.

Our findings that an imitative bias is not present following counter-imitative experience (i.e., the second block of reinforcement trials in experiment one and experiment two), suggests that sensorimotor experience can eliminate imitative biases, complementing evidence from a range of other human studies and one finding with dogs (Catmur et al., 2008; Heyes et al.,

2005; Range et al., 2011). However, any conclusions concerning a lack of a strong disposition to imitate rests on null findings which must be interpreted with caution (Sainani, 2013). Furthermore, Carlos, one of the two monkeys in experiment two, did perform significantly better when rewarded for compatible responses (see Figure 2), and so it may be that an imitative bias can be maintained in certain contexts. Carlos was the only monkey in experiment one who reached the predetermined learning criterion in the initial learning block, and this initial reinforcement may have led to a persistent advantage for imitative rules across subsequent trials, conducted more than 10 months after this initial reinforcement was received. In contrast, Chico, the monkey who did not display a bias for any particular rule in experiment two, while the best performer in his initial block of incompatible learning in experiment one, did not reach the learning criterion and so was not reinforced preferentially for incompatible response to the same extent as his compatibly reinforced counterpart. This difference in reinforcement history in the first part of experiment one (see Table 1) may explain the individual differences in experiment two, but we stress that this post-hoc interpretation is highly speculative. Overall, the failure to identify strong imitative biases suggests that relationships between sensory and motor representations of actions in monkeys are malleable, at least in some contexts.

Given the marginal difference between conditions at the first stage of this experiment, it may not be particularly surprising that initial experience of reinforcement had the effect of minimizing an imitative bias at other stages of this study. However, this effect is notable when considering the persistence of some SRC biases in other domains. For example, one classic study of a traditional stimulus-response compatibility effect (the Simon effect) in adult humans found that compatibility effects were still present in some cases after more than 1500 trials (Fitts & Seeger, 1953), suggesting that when there is strong dimensional overlap in S-R pairings, compatibility effects persist in the face of considerable experience. Of course, there

may be greater overlap in the characteristics of some other S-R pairings examined with this procedure (e.g., spatial orientation; Simon & Rudell, 1967). In contrast, and as highlighted earlier, for certain actions (including the mouth action used in this study) the perceptual information available when observing one's own actions and those of another often do not correspond. Instead, in the case of some opaque actions, the associations between stimuli and action responses must be the result of either specific experience linking these (analogous to the learned associations that result in phenomena such as the Stroop effect; Stroop, 1935), or would need to be present from birth in the form of a multimodal matching system (e.g., Meltzoff & Moore, 1997). It should also be emphasized that the absence of an imitative bias following incompatible sensorimotor experience is not irreconcilable with the presence of a multimodal action matching system that exists at birth, as later learning may both inhibit or facilitate a pre-existing imitative bias, and indeed proponents of neonatal imitation accept that later learning is likely to influence imitative ability (Marshall & Meltzoff, 2014).

Examples of imitative learning may be rare in capuchin monkeys, but imitation recognition and the role of imitation in facilitating affiliation are also worth considering briefly. For example, capuchins and macaques recognize when the actions of human experimenters correspond to their own and seem to display affiliative behaviors towards these individuals (Paukner et al., 2009; Sclafani, Paukner, Suomi, & Ferrari, 2015). If the mechanism that links observable action to an executed action is forged through associative learning then it is possible that monkeys that have been trained to respond in counter-imitative ways may show increased interest and affiliation towards those that perform contingent non-matching actions. However, if it is discovered that imitation's role in affiliation is still present following incompatible training, then this would call into question the proposal that sensitivity to action matching is purely the result of experience. It may also be the case that the mechanisms underlying

imitation's role in learning and affiliation have different origins. Nonetheless, SRC tasks may in the future be a useful tool in examining the link between imitation and affiliation.

Overall, this study contributes to a growing understanding of action imitation in primates and the impact of experience on imitative behavior. However, this is only a first step towards understanding the types of experiences that may impact upon imitative ability in primates, and future work is necessary to understand the full extent of experiences' role not only in the elimination of imitative effects, but in the development of these effects. Further work incorporating action SRC paradigms with New and Old World primates may provide unique insight into imitative effects in nonhuman primates, and could be used to test a variety of hypotheses related to the extent and ontogeny of action matching in nonhuman animals in general.

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Table 1.

Descriptive data from stimulus response compatibility (SRC) trials 1-500 for each monkey (320 trials for Kato and Sylvie) in both conditions with trial success coded as a binary variable (1 represents a successful response and 0 an unsuccessful one). This measure is the equivalent to the proportion of correct responses in a learning block. Standard error of the mean is included in brackets. See Figure 1 for a graphical representation of totals.

Rule rewarded in 1st Reinforcement Block		Trials per learning block	Mean Trial Success (SE)	
			1st Block	2nd Block
Pedra	Incompatible	500	.506 (.022)	.522 (.022)
Figo	Incompatible	500	.500 (.022)	.478 (.022)
Chico	Incompatible	500	.572 (.022)	.444 (.022)
Kato	Incompatible	320	.500 (.028)	.478 (.028)
Total	Incompatible	1820	.521 (.012)	.481 (.012)
Carlos	Compatible	500	.658 (.021)	.484 (.022)
Micoe	Compatible	500	.562 (.022)	.502 (.022)
Inti	Compatible	500	.516 (.022)	.478 (.022)
Sylvie	Compatible	320	.512 (.027)	.500 (.028)
Total	Compatible	1820	.567 (.012)	.490 (.012)

Table 2.

A Generalised Linear Mixed Model with a binomial error distribution and logit link function is reported below. Trial performance (correct/incorrect) was examined as the dependent variable, and condition (compatible/incompatible) and order of learning (1st block/2nd block) were included as fixed effects. Individual monkey was included as a random intercept in the model and session number was included as a random slope.

Random Effects	Variance	STD		
Monkey (intercept)	0.0087	0.0933		
Session	0.0137	0.1169		
Fixed Effects	Estimate	SE	z	p-value
Intercept (Order = First, Condition=				
Compatible)	0.4499	0.1315	3.421	<0.001
Incompatible (when order = First)	-0.2589	0.1253	-2.067	0.039
Order (when condition = Compatible)	-0.5298	0.1366	-3.879	<0.001
Order * Condition	0.2981	0.1481	2.012	0.044

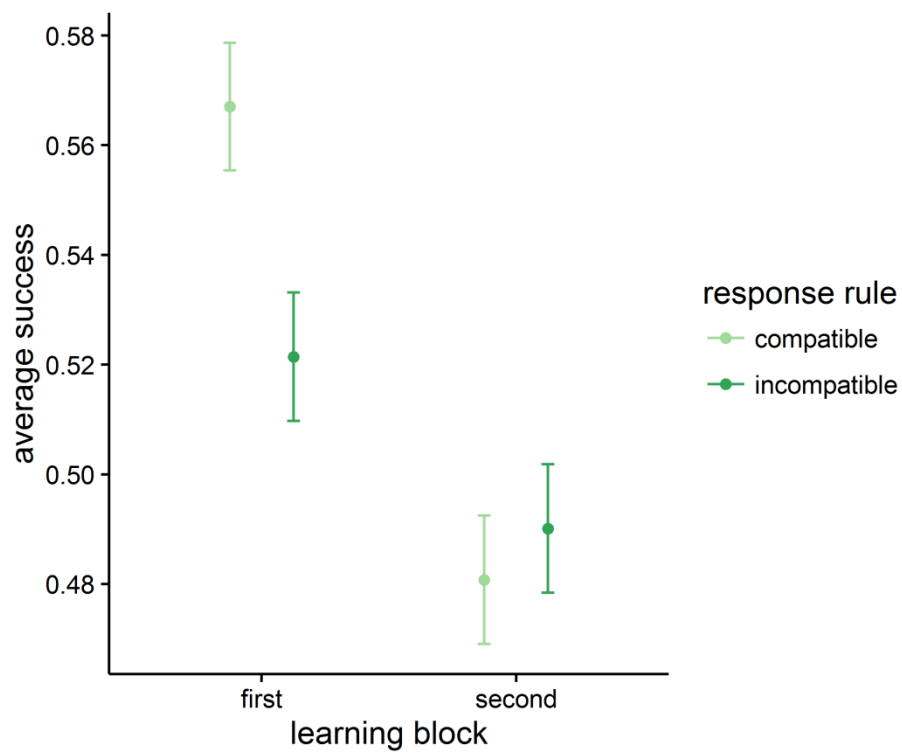


Figure 1. Mean proportion of correct responses in the first 500 trials for compatible and incompatible conditions when associative rules are first learned and following rule reversal. Error bars represent standard error of the mean.

Table 3.

Number of trials completed before each monkey reached learning criteria for each learning block. The first letter of the rule learned is in brackets after the trial number (compatible =c; incompatible =i); e.g., Carlos began learning the compatible rule while Chico began with the incompatible rule.

Number of Trials Before Reaching Criterion			
Learning Block	Carlos	Chico	Total
1	200 (c)	204 (i)	404
2	166 (i)	267 (c)	433
3	60 (c)	551 (i)	611
4	280 (i)	541 (c)	821
5	235(c)		
Total	941	1563	2269

Table 4.

To examine whether condition (compatible/incompatible) and monkey (Chico/Carlos) influenced trial success over the first 60 trials of each learning block, we created a Generalised Linear Model with a binomial error distribution and logit link function. The full model is reported below.

Fixed Effects	Estimate	SE	Z	p-value
Intercept (Monkey = Carlos, Condition=				
Compatible)	0.4754	0.1878	2.532	0.011
Incompatible (when monkey = Carlos)	-1.5740	0.2823	-5.576	<0.001
Chico (when condition = compatible)	-1.2063	0.2706	-4.457	<0.001
Monkey * Condition	1.7223	0.3923	4.390	<0.001

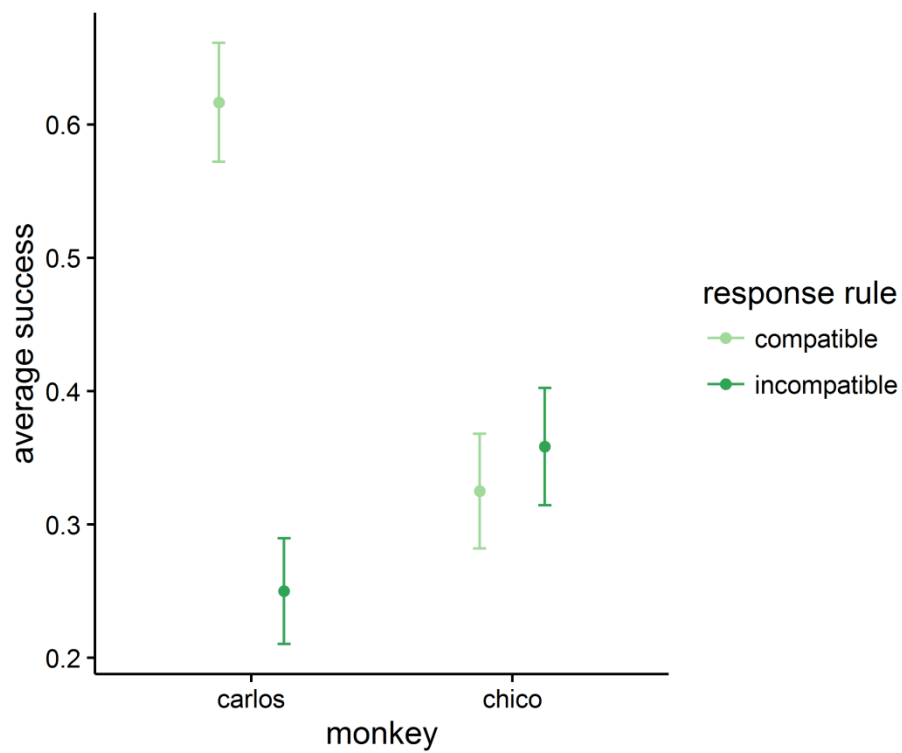


Figure 2. Mean proportion of correct responses in experiment two over the first 60 trials of each learning block for both subjects (Carlos/Chico) differentiated by response rule. Error bars represent standard error of the means.